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Conceptual Challenges and Directions for Social Neuroscience

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Abstract

Social neuroscience has been enormously successful and is making major contributions to fields ranging from psychiatry to economics. Yet deep and interesting conceptual challenges abound. Is social information processing domain specific? Is it universal or susceptible to individual differences and effects of culture? Are there uniquely human social cognitive abilities? What is the "social brain," and how do we map social psychological processes onto it? Animal models together with fMRI and other cognitive neuroscience approaches in humans are providing an unprecedented level of detail and many surprising results. It may well be that social neuroscience in the near future will give us an entirely new view of who we are, how we evolved, and what might be in store for the future of our species.

Introduction

Social neuroscience was first coined as a term and proposed as a field in 1992, at the beginning of the Decade of the Brain, in an article that stressed the need to apply an interdisciplinary, multilevel analysis to understanding social behavior and cognition (Cacioppo and Berntson, 1992). Yet at that time, one of the major tools available to study the social brain–neuroimaging–was limited. Following earlier studies using positron emission tomography (PET), it took nearly a decade for functional magnetic resonance imaging (fMRI) to establish itself as the most prominent approach in social neuroscience. Work in the 1990s instead progressed along diverse lines, including a variety of seminal studies on affiliative behaviors in animals as well as on issues related to clinical health and socioemotional processes. Some of the most influential studies were based on focal brain lesions in both monkeys and humans, but these studies could only be carried out by relatively few laboratories. There was also still a substantial public resistance to the very idea of social neuroscience or indeed any approach that people associated with sociobiology. Not surprisingly, at that time genetics somewhat overshadowed neuroscience, both in terms of the science done and in terms of the socioethical objections to it.

That has changed. Although it took several more years for fMRI studies to follow the call of Cacioppo and Berntson's initial article (Cacioppo and Berntson, 1992), the year 2001 saw the publication of the first edited volume on social neuroscience led by the same authors (Cacioppo et al., 2001), as well as a seminal article outlining explicit synergies between cognitive neuroscience (by then well defined) and social psychology (Ochsner and Lieberman, 2001). By now everyone is aware that the neurobiology of social behavior (henceforth, "social neuroscience") is a burgeoning field: there are numerous conferences, calls for funding proposals, even new journals and societies attesting to its popularity (for instance, the new society for social neuroscience, www.s4sn.org). Its impact has spread from social psychology (Ochsner and Lieberman, 2001) to the study of decision making (as in the investigation of

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social factors in neuroeconomics) (Camerer, 2003; Fehr and Camerer, 2007) to the study of numerous psychiatric illnesses (from autism to schizophrenia) (Cacioppo et al., 2007) and highlighted a number of animal models (see Sokolowski [this issue of *Neuron*]). So dominant is the approach in the behavioral and social sciences, in particular the use of fMRI to probe cognitive processes, that it threatens to displace traditional behavioral economics, social psychology, and even aspects of political science.

Many of the foundational issues that the field debated over a decade ago still remain, and new ones have been added (Adolphs, 2003b). These issues are challenges not only for the study of social cognition, but important for cognitive neuroscience generally and critical to our understanding of the human mind in both health and disease. It is probably fair to say that the technical advances and the sheer accrual of data are rapidly outstripping our ability to understand it all. In response to the ethical concerns around cognitive neuroscience in general, there is now a society for neuroethics. In response to methodological concerns about the statistical analyses associated with fMRI, there is now a healthy corpus of writings (e.g., Kriegeskorte et al., 2009; Vul et al., 2009) as well as numerous responses and universal awareness of the issues. But conceptual challenges remain often unarticulated, a situation exacerbated by the breakneck pace of research, which leaves one little time to step back from the deluge of weekly papers to read and reflect on the questions. I step back here and highlight some of the key questions, important approaches, and conceptual challenges in social neuroscience. Many of them make direct contact with the other reviews in this special issue. While I provide numerous examples from the literature throughout, this is not intended to be an in-depth review of social neuroscience (Adolphs, 2003a, 2009; Amodio and Frith, 2006; Frith, 2007; Moll et al., 2005; Saxe, 2006b) but rather a more theoretically oriented discussion of its conceptual foundations and challenges, with an emphasis on studies in humans.

Social Perception

Social behavior is as ubiquitous as it is essential, since every species has more than one of its kind and depends on others of its kind. In a very broad sense, all life is social, a truism that applies equally to phylogenetic observations as it does to everyday life for *Homo sapiens* in particular. These considerations threaten to equate social neuroscience with all of neuroscience, with nothing proprietary left to define the field. However, a quick sketch of how socially relevant information is processed begins to show how social neuroscience is distinct and sets the stage for the conceptual themes and challenges we review here. There are three broad stages of social information processing to briefly consider: perception, cognition, and regulation (Table 1).

We can begin with the transduction and perception of social information. Detection of pheromones, somatosensation of affective touch, auditory perception of conspecific songs in passerine songbirds, and visual perception of faces in sheep and primates, to name just a few examples, all draw upon features of perception in general. But there is already a difference from perception in general here: at least some aspects of these examples of social perception feature “labeled line” pathways, or “modular” central representations, that are dedicated to that particular type of stimulus. Pheromonal communication through the vomeronasal organ is perhaps the clearest example, since this entire sensory modality is specialized for social information beginning at the periphery (Insel and Fernald, 2004). A good analogous example in insects is the recent discovery that 11-cis-vaccenyl acetate is a male-specific pheromone for aggressive behavior in flies, acting through an equally specific olfactory receptor (Wang and Anderson, 2010). A similarly specific molecule and its neural signature in the olfactory system has been identified in mice, in this case for mate attractiveness through the molecule's presence in mouse urine (Lin et al., 2005). And there is a plethora of model systems in which the olfactory signature of a conspecific is linked in memory to specific social behaviors, such as the well-

known affiliative behaviors of prairie voles (Insel and Young, 2001) and bonding between sheep ewes and their offspring triggered by parturition (Broad et al., 2006). These last two examples involve actions of the peptide oxytocin, which modulates human social behavior (Kosfeld et al., 2005) and neural responses (Baumgartner et al., 2008) as well and is a current hot topic of social neuroscience investigations. While the role of pheromones in human social behavior is likely to be modest compared to other sensory modalities, and the detailed mechanisms remain debated, there is a growing set of behavioral and neuroimaging studies examining this topic as well. Many of these instances are likely mediated through the main olfactory system rather than the vomeronasal system, which is also a major conduit for social perception across a wide range of mammalian species (Sanchez-Andrade and Kendrick, 2009). The existence of such "labeled lines" for social perception is probably driven by the fact that the stimuli are generated by conspecifics, decoupling them from other environmental stimuli and facilitating the coevolution of dedicated channels for social communication.

Complex patterned stimuli that are ingredients in social communication, while not so specialized in their perception at the very periphery, also feature specialized central systems for their perception and representation: song-selective neurons in the forebrain nuclei of passerine songbirds (Margoliash, 1983) and face-selective neurons in the temporal lobe of primates (Tsao et al., 2006) and sheep (Tate et al., 2006) are examples. As with the social perception of odorants, these are beautiful model systems for studying sensory processing and perception for social behaviors. Once again, they have human analogs: for instance, a specific region in the ventral temporal lobe of humans that is selectively activated by the sight of faces (Kanwisher et al., 1997; McCarthy et al., 1997), a topic we take up in more detail below.

Social touch is an interesting somatosensory channel that has received some recent attention in studies in humans. Beginning with observations of patients with rare demyelinating diseases who could perceive a caress as pleasurable but fail to localize it on their body (Olausson et al., 2002), it has become clear that there are labeled-line pathways from the skin to regions such as insular cortex that transmit affective properties of social touch (Löken et al., 2009; Morrison, 2009). This modality is ripe for deeper investigation in other species, especially given the well-known importance of social touch for normal development in mammals (Francis et al., 1999; Harlow and Harlow, 1962) and the importance of social grooming for maintaining social relationships in nonhuman primates (Dunbar, 2008).

Thus, already at the level of perception (for pheromones and affective touch, already at the level of sensory transduction), there is evidence for domain-specific processing of social information. There remain debates over how exactly to describe such specialized processing —does it meet criteria for Fodor-style modularity (Fodor, 1983)? Is it domain specific (specialized for a circumscribed class of stimuli) or process specific (specialized for a particular type of computation) (Tarr and Gauthier, 2000; Yovel and Kanwisher, 2004)? In terms of its neural substrates: are there regions and systems neuroanatomically specialized for social perception? At the most peripheral levels, the answer seems to be a clear "yes." There are specialized transduction channels for social communication as noted above. On the other hand, there are narrow-bandwidth channels for many stimuli; different classes of photoreceptors and mechanoreceptors all feed processing channels that are to some degree segregated both functionally and anatomically. So while social perception may occupy some unique channels for sensory processing, the fact that it does so is not unique.

Social Cognition

Social cognition may be another matter. Once we go beyond processing driven primarily by the sensory input and consider the attributions and inferences that we make in order to construct a richer representation of the distal stimuli that caused the sensory input, social cognition recruits processes that seem to find no analog in nonsocial cognition. We quickly recognize

how somebody is feeling, what they intend to do, and whether they are friend or foe by making such inferences. Indeed, we do it so compulsively and automatically (as borne out in our propensity to anthropomorphize), that it is sometimes difficult to appreciate the rich elaboration that is required. An important topic in social psychology that blossomed in the 1980s (Fiske and Taylor, 1984), social cognition features a very rich repertoire of attributions that make us see the world imbued with social meaning. When we perceive a facial expression in a particular context, we not only see the face and the context, but immediately generate knowledge about something that we can never observe directly: the mind of another person. So-called "theory of mind" is a large topic in social neuroscience, with a huge literature questioning whether it exists in animals other than humans (Penn and Povinelli, 2007; Premack and Woodruff, 1978; Tomasello et al., 2003), showing how to study it using fMRI (Saxe, 2006b), and demonstrating its impairment in autism (Baron-Cohen, 1997; Frith, 2001); we take it up in more detail below.

Of course, inference and filling-in are commonplace in sensory processing—as anybody who has seen the "edges" in an illusory Kanisza triangle will testify. But in all those cases, what is filled in is more of the same stuff, just extended in space and/or time. What is filled in for the case of social cognition is another kind of stuff: we see a person's face, and we fill in the unobservable psychological states of a person by which we attempt to predict their behavior. The case is also disanalogous to filling-in with causal perception. We do project the future trajectories of objects, and we fill in their physical properties from which we infer such projections. But it is only when we engage with social stimuli that mental attributes are inferred, typically with a concomitant sense of reciprocal involvement and normative evaluation that finds no obvious parallel in nonsocial stimuli. Plausibly, there are levels of intermediate inference between the physical causal attributions we make and the full-blown attributions of another conscious mind—such as attributions of agency and animacy that apply to a wide range of other organisms and that likely emerge earlier in development and phylogeny than do attributions of minds as such.

Perhaps one of the best examples of a social inferential process is the currently hot topic of action perception through simulation, which is thought also to be related to emotional simulation in empathy (de Vignemont and Singer, 2006). Intentional actions can be distinguished from nonintentional actions in several primate species (Wood et al., 2007), and primates have so-called "mirror neurons" that respond both when the animal executes a goal-directed action and when it observes someone else perform that same action (Rizzolatti and Craighero, 2004). This mechanism may underpin aspects of social learning and constitute a key component of social cognition (Gallese et al., 2004). Again, in the absence of anthropomorphizing, it finds no clear analog in nonsocial cognition.

Of course, one can argue with this view of social cognition as special and see the story instead much like what I sketched for social perception: inference, attribution, and filling-in are of a special sort for social stimuli, but the general computational process is ubiquitous in how the brain processes information. Perhaps the most decisive evidence in favor of the view that social cognition is special is neurobiological: different brain structures are involved. Social neuroscience has now identified a network of structures that all seem to come into play disproportionately when we think about other people, as opposed to when we think about nonsocial objects: it includes medial prefrontal cortex, sectors of the temporoparietal junction, regions containing "mirror neurons," and others (Adolphs, 2009; Amodio and Frith, 2006; Saxe, 2006b). While the precise anatomical delineation of this so-called "social brain" remains a topic of intense investigation (one which we discuss further below), its fuzziness does not detract from its prominent role in carving out what is special about social cognition (indeed, some recent proposals argue that this will be *the* basis for delineating social cognition as distinct [Mitchell, 2009]).

Social Regulation

Finally, we also are able to step back and regulate and control our thinking and our behavior using metacognitive abilities. This certainly plays a large role in human social behavior but does not appear to be unique to the social domain, since we have to reflect on all aspects of our behavior and control all kinds of thoughts and actions all the time. It is, however, quite possible that the evolution of our extensive cognitive control, especially in relation to emotion regulation, was driven by social factors—notably, the advantage in being able to deceive others. I mention regulation here primarily for completeness and because of the noted likely importance especially of emotion regulation, a topic of great interest to those studying social development and also a major contributor to social dysfunction when impaired (Davidson, 2002; Ochsner and Gross, 2005).

This brings us back to a question related to the one we posed at the beginning of our discussion concerning the boundaries of the field of social neuroscience: is all social processing emotional? The learning and regulation of emotions features very prominently in social neuroscience (Olsson and Ochsner, 2008). Recognition of emotions is a very popular topic of study and constitutes an important aspect of social communication. And the so-called social or moral emotions are precisely that—they arise only in a social context. It may be that the complexity of the social environment has driven the emergence of more finely differentiated emotions, and those are the ones we typically have names for and consider emotions, even though other states such as hunger and thirst play a similar functional role and share many of the same neural substrates (Panksepp, 1998). While emotion and social cognition are closely intertwined, it also seems that many aspects of social cognition do not involve blatant emotional reactions—we can recognize the identity of a person from their face or decide on a particular strategic course of deliberate action without the obvious involvement of emotions. An important question for the future is therefore why, when, and how emotion participates in social cognition.

This brief review of some of the broad components of social information processing argues that the brain treats social stimuli in many ways differently from nonsocial stimuli and suggests that social neuroscience studies a select set of processes that are distinguished computationally, in terms of their content, and in terms of their underlying neural substrates. It also points to questions we should ask if we want to conduct investigations in social neuroscience. I discuss several conceptual issues further below but first briefly consider an overarching question regarding why anybody would find this interesting in the first place.

Why Is It Interesting and Important to Investigate Social Neuroscience?

Any researcher in the field should be able to provide an answer to the question of this section and defend it; any student in the field or thinking about going into the field should be asking the question. In fact, answers are easy to come by.

Clinical Relevance and Individual Differences

One answer arguably underpinning most funding to the field is that it is of patent clinical relevance, and there are many examples ranging from psychiatric and neurological disease to healthy adolescent development and aging. It will be particularly important to trace impairments in social functioning to deficits in specific stages of social information processing. Looking back at the stages of processing we briefly outlined above, we can ask the question to what extent a psychiatric illness might result from impaired perception, cognition, or regulation. For instance, many mood disorders are thought prominently to feature dysfunction in emotion regulation, and there are important discussions about whether autism might result

from sensory processing impairments or from motivational impairments (the latter, in the context of a developmental disorder such as autism, may in turn give rise to the former).

The diseases that have been highlighted include those for which social dysfunction is part of the diagnostic criteria, such as autism or social phobia, but in fact nearly every psychiatric illness listed in DSM-IV includes aspects of social functioning as a core component of real-life impairments. Mood disorders in general severely affect our ability to interact with other people, as do schizophrenia, personality disorders, drug addiction, and anorexia nervosa. Neurological diseases are also fast to list off: lesions in many brain structures impair social cognition, with perhaps the largest population consisting of those with damage to the prefrontal cortex arising from traumatic brain injury, e.g., through automobile accidents (Anderson et al., 1999). Neurode-generative disorders such as Parkinson's, Huntington's, and Alzheimer's disease all impact social functioning, in some cases by disproportionately damaging regions of the “social brain” (e.g., in frontotemporal dementia [Kipps et al., 2009]). Many of the psychiatric diseases are on a continuum with variability in the healthy population, and overlapping sets of neural structures may be responsible for individual differences and diseases of social cognition. To give just one intriguing recent finding in this vein: using a neuroeconomics approach, it was found that people with borderline personality disorder cooperate less with others and that this is correlated significantly with abnormal activation of the insula to the perception of social signals (King-Casas et al., 2008).

These broad perspectives are exciting, because they suggest that we can understand illness in part through understanding normal individual differences and development–or, indeed, well-justified animal models. They are also theoretically exciting because they raise questions about the source and adaptive value of such variability. Is there an advantage to have evolved considerable variability in social behavior? Do other animals show similar variability and similar disorders of social behavior? These questions are particularly acute these days because there is some evidence that certain diseases of social cognition (e.g., autism) may be increasing in prevalence and because it is clear that the modern-day social environment of humans is very different from the social environment in which we evolved. To what extent is the human “social brain” maladapted for the modern social environment we have created for it?

Collective Behavior

This brings us to a second answer to our original question. Social neuroscience is interesting and important for understanding collective human behavior, ranging from the positive (cooperation and altruism) to the negative (conflict and war). This angle is of particular interest to anthropologists, economists, and comparative biologists. From a comparative perspective, it is intriguing to consider the evolution of collective behavior. There are many examples where behaviors at the level of individuals clearly contribute to collective survival, such as in schools of fish or flocks of birds. These behaviors can be modeled by rather simple local rules implemented in the brains of the individual that, once selected, render the behavior of the entire group adaptive (Couzin, 2009).

However, much group behavior features a fundamental conflict between competition for limited resources (food, mates) and cooperation needed to compete on a larger scale. While it might seem that within-group cooperation and between-group competition should be the stable solution, within-group cooperation is always susceptible to individual free riders that take advantage of the group's resources at the expense of other group members. Theoretical, simulation-based, and empirical studies have all provided strong reasons for thinking that cooperation in humans is complex and polymorphic. Populations of reasonably large size appear to evolve toward a dynamic mixture of types of individuals–some cooperate, some defect, and some are intermediate (Nowak and Sigmund, 2004). This picture fits well with empirical data as well (Kurzban and Houser, 2005) and also with emphasis on individual

differences. Indeed, it is likely that it will be linked in part to particular genetic polymorphisms that underlie these individual differences. One ingredient of particular recent interest is the finding that costly (altruistic) punishment to enforce cooperation can emerge and stabilize cooperation, likely an ingredient essential to many aspects of large-scale human social behavior (Boyd et al., 2003; Fehr and Gaächter, 2002).

The new field of neuroeconomics has gathered tremendous momentum and excitement in identifying the neural mechanisms behind collective behaviors such as cooperation, punishment, and altruism using tools from economic decision theory (Fehr and Camerer, 2007; Kable and Glimcher, 2009; Rangel et al., 2008). For instance, the above-mentioned phenomenon of altruistic punishment has been studied using neuroimaging, with the finding that the ventral striatum is activated when third parties punish what they view as unfair behavior in others. This result can be interpreted as resulting from our motivation toward altruistic punishment by the prospect of feeling satisfaction, a mechanism analogous to that which motivates behavior to obtain expected rewards (deQuervain et al., 2004). A related earlier finding showed that unfair offers made in a trust game resulted in rejections behaviorally and were correlated with activation of the insula, a region known to represent pain and disgust, again suggesting that basic reward-related processes also come into play during social interactions (Sanfey et al., 2003). Similarities in the processes behind reward learning and social interactions have been found in many other studies as well: for instance, temporal shifts in anticipating trusting behavior mirror those seen in anticipating rewards (King-Casas et al., 2005). Neuroeconomic approaches to social neuroscience are forging a major quantitative contribution to the investigation of psychiatric illness and individual differences that we noted in the previous section as well. For example, specific neural signatures have been identified in the brains of people with autism when they engage in an economic trust game (Chiu et al., 2008), and individual differences in altruistic behavior are correlated with individual differences in activity within dorsolateral prefrontal cortex, a region known to be important for cognitive control (Hare et al., 2009; Knoch et al., 2009).

If the advantage to cooperate is large, such as in species where group selection may operate, eusocial behavior can emerge: the highly organized division of labor and reproduction seen in species such as ants, termites, and bees (Figure 1). Only two species of mole rats, a fossorial rodent, have evolved eusocial behavior in mammals, possibly due to the very specialized adaptive challenges in securing a stable food supply in those species. Other mammalian species have instead evolved more flexible and less stable forms of collective behavior–in primates, ones that involve deception and strategic behavior. It is an interesting question whether human evolution would eventually result either in extinction of our species or in a species with stably cooperative social behaviors reminiscent of eusociality.

Insights for Basic Research

There are also two less applied and more basic reasons why it is interesting and important to do experiments in social neuroscience. One valid reason is that the study of social information processing will inform cognitive neuroscience, and neurobiology, more generally. A second, often more personal, reason is that it is fascinating to ask how and why the human mind appears to be so different from the minds of all other animals–how and why do we have language, self-reflection, and conscious experience in a way other animals very likely do not (see Byrne and Bates [this issue of *Neuron*])? Often implicit here is the assumption that whatever it is that is “uniquely human,” it has to do with our social cognitive abilities. At the heart of the puzzle is our ability to step back from the current experience of the world in which we are caught up, and by doing so to generate a concept of the distinction between subject and object, between mind and world. This ability is presumably also related to our concern for ourselves and our species, because it gives us a glimpse into our mortality. It seems unlikely that any other animal

feels a need for religion or can contemplate suicide, just as it seems unlikely that any other animal can worry about the future of its species, let alone attempt to intervene in a directed way; on the other hand, evidence to support our intuitions in this regard is extraordinarily difficult to come by. Answers to this aspect of social neuroscience will recast our understanding of who we are, where we came from, and what we might become.

Finally, it would be an omission not to acknowledge that of course understanding social behavior requires much more than cognitive neuroscience, more than neurobiology, and indeed more than biology. This realization is one reason the field is so exciting: it is vibrantly interdisciplinary. We can ask questions from within philosophy, we can investigate social behavior with models that require no biological data at all, and we can engineer social robots. Social neuroscience is not, and cannot be, the only way to investigate social behavior; but it will be indispensable if we want to uncover the underlying mechanisms, understand how individual differences arise, and formulate targeted interventions for treating disease.

Current Themes and Debates

I will consider primarily one overarching question, which spawns several subquestions, each of them topics and challenges in social neuroscience. The question is: What is the mapping between brain structures and psychological processes?

For behavioral, systems, and cognitive neuroscience, this is arguably the key question of all. Parts of it are straightforward to address, other parts are extremely difficult. A starting point for providing an answer is historical. When Franz Josef Gall conceived of phrenology in the late 1700s, it became wildly and derisively popular in America in the early 1800s. One reason for the popularity is that it provided a concrete basis for psychology–it carved the mind up into neat little modules (27 of them, to be exact) and put them in their place in the brain (Gall's magnum opus was a six-volume treatise on the idea published between 1822 and 1825). Gall, Spurzheim, and their followers argued that specific mental “organs” were localized in specific brain regions (an extreme form of anatomical modularity) and that, moreover, the degree of the mental ability or propensity was directly related to the size of the responsible brain region, something that could be inferred from palpating the bumps on people's skulls. While essentially every aspect of phrenology was grossly incorrect in its details, the approach was both attractive and in fact reasonable. What have we learned since then? I think there are two important lessons: first, no single brain structure maps any central psychological process we can conceive of, so it is a challenge to delineate the neuroanatomy; second, it is unclear what psychological processes to map in the first place.

What Are the Brain Structures?

It is easy to see that this question, while in principle straightforward, is empirically extraordinarily difficult. Concepts such as the limbic system, and even otherwise well-regarded structures such as the amygdala (Swanson and Petrovich, 1998), have been cast into doubt as the right way to carve up the neural tissue. The idea that there are specialized structures that constitute a neural system for processing social information, the so-called “social brain” (Brothers, 1990), has guided social neuroscience studies in humans for the past two decades and led to a collection of structures that regularly turn up in fMRI studies of social cognition (Adolphs, 2009; Frith, 2007; Saxe, 2006b). Certain structures, such as medial prefrontal cortex, turn up so reliably across studies and across different social processes that they have been suggested by some as the neuro-anatomical basis for specifying a proper domain for social psychology (Mitchell, 2009). But the exercise of outlining sets of structures in these studies has also begun to outline the challenges faced by any attempt to delineate neuroanatomically a system for processing social information. The relevant brain structures

almost never map cleanly onto some macroscopic region or Brodman Area. Instead, subregions, or subpopulations of neurons within a region, will be the relevant level of grain.

Of course this progression is found within all cognitive neuro-science, not only social neuroscience: regions originally postulated to implement some process become progressively more fractionated as techniques with better spatial and temporal resolution arise. One recent example is a debate about the role of the temporoparietal junction (TPJ) in subserving “theory of mind,” our ability to infer mental states from descriptions or observations of people's actions. On one side of the debate it was argued that the TPJ is selectively activated by theory-of-mind tasks (Saxe and Powell, 2006); on the other side, it was argued that this cortical region subserved a more general function in directing attention (Mitchell, 2007). The debate is now partly resolved by the finding that separate sectors of the TPJ subserved these two competing processes, so closely adjacent that they could not be spatially resolved in the prior studies (Scholz et al., 2009).

A similar fractionation into smaller regions has occurred for many other structures, in the case of social cognition in particular for regions of the prefrontal cortex (Barbey et al., 2009). However, the felt need to map processes onto spatially defined regions is giving way to multivoxel analyses, in which classification algorithms from machine learning are applied across the brain to decode processes without requiring clean spatial segregation (Mur et al., 2009). This approach emphasizes *how* the brain represents social information–the discriminations it makes–without analyzing *where* (although decoding approaches can also be applied in a searchlight fashion to get some spatial information). Even so, BOLD-fMRI will present fundamental limitations that preclude findings such as those obtained from single-unit electrophysiology. For instance, single neurons in the human temporal lobe have been found to encode very high-level semantic knowledge about specific people: they respond both when shown the face of a famous actor and also when reading the actor's name (Quian Quiroga et al., 2009). No equivalent responses have yet been decoded using fMRI, and given the very sparse and diverse neuronal response categories, it seems unlikely that this can be achieved.

A conceptually difficult challenge is posed by the realization that no brain structure, or subpopulation of neurons, operates in isolation: we need to look at connected systems, whose boundaries are even harder to define. A full understanding of social information processing needs to acknowledge that the processing is not only spatially distributed but also temporally dispersed. This is now well known, although the bulk of lesion and functional neuroimaging studies nonetheless still produce data that are phrenological in flavor by concentrating on a single region–often without even knowing from where it receives its inputs nor what its projection field encompasses. The advent of recent tools for exploring structural and functional connectivity in the brain is having some effect on the data produced, but it is still difficult to think about processes as implemented in dynamic brain networks. On the other hand, descriptions in this spirit have been around for quite a few years in computational neuroscience, and some empirical studies have generated such a picture as well (Laurent, 2002). The problem has been linking such dynamic network descriptions to processes at the systems and cognitive level in mammals. Yet the need for a distributed-systems approach is widely acknowledged; even Leslie Brothers' original description of the “social brain” (Brothers, 1990) outlined a set of distributed structures. A good example of such a direction in social neuroscience is the discovery of connected patches of temporal and frontal cortex that process faces in primates (Moeller et al., 2008). Ultimately, we will need an account of how such distributed neuronal representations, at particular points in time, make explicit social information that can be used to guide behavior.

An even more challenging question is whether the body and the external environment participate in psychological processes, taking social information processing outside of the brain

alone. There are patent ways in which this happens all the time, such as when we use calculators, computers, or pencil-and-paper scratchpads to offload information processing from brain to environment. There are highly contentious ways in which (to some thinkers) it is conceivable that conscious experience itself somehow depends on more than just brain events (Clark and Chalmers, 1998). In fact, there are reasonable arguments to think that this is not only possible but necessary in order to ground the otherwise meaningless events that happen in the brain: they must be connected to the world in some way (the so-called classical "symbol-grounding problem"). These discussions are continuous with philosophy of mind and nonspecific to the social domain; they constitute one of the most vigorous current lines of research in "embodied cognition." But they have been highlighted most visibly within social neuroscience. Investigations of empathy, simulation, and the "mirror neuron system" all postulate the engagement in an observer of some mechanisms similar to those seen in another person, in virtue of which social knowledge can be generated. The topic originated in the discovery of "mirror neurons" that respond both to the execution and observation of a specific action in monkeys we noted earlier (Rizzolatti et al., 2001) and were quickly adopted by cognitive neuroscience to explain action observation more broadly in humans as well (Gallese and Goldman, 1999). While the original focus, and still the best correspondence between monkey and human data, is restricted to goal-directed actions (Rizzolatti and Fabbri-Destro, 2008), social neuroscience studies using fMRI in humans have considerably broadened the scope of such mirroring mechanisms. For instance, human fMRI studies have found that the observation and imitation of facial expressions engage overlapping brain regions (Carr et al., 2003), that observing a spouse experience pain activates regions overlapping with those when one experiences pain oneself (Singer et al., 2004), and that more generally the experience and recognition of emotions draw on shared mechanisms (Bastiaansen et al., 2009; Goldman and Sripada, 2005). A related thread, this time originating from the perceptual end rather than the motor end, is found in the idea that concepts are grounded in the representations through which they were acquired (Barsalou, 1999). All of these accounts aim toward some kind of grounding of central representations in more peripheral representations, whether sensory, motor, or both. Yet the literature on "embodied" or "situated" social cognition is typically rather vague as to the exact claims.

Is embodiment thought to literally involve the body, or just central representations of the body? Are perceptual or motoric representations in the brain thought to be merely involved, or constitutive of social cognition? These and other questions require careful dissection, have engaged philosophers as well as cognitive neuroscientists (Goldman and de Vignemont, 2009), and have to some extent continued a long-standing debate about the very status of simulations (Saxe, 2005), reminiscent in many ways of the debate about the status of visual imagery (Kosslyn et al., 2003). In both of those cases, some thinkers find it intuitively plausible that there are central, often amodal, representations that function much like sentences: they represent by description (through the functional properties of symbols). Other thinkers find it inconceivable how there could be only such representations, and believe that, at some level, the symbols need to merge with what they represent: they represent by resemblance, much like a map. These issues hark back to provocative proposals about how all abstract thought itself might be based on bodily experience (Lakoff and Johnson, 1999).

There is also a more recent and specific debate about the conditions under which simulation-like mechanisms of social cognition might be deployed, as contrasted with so-called "theory-of-mind" mechanisms, which are presumed to generate similar knowledge of other minds, but in a more deductive fashion that does not require actual simulation. There is now some acknowledgment that there are multiple mechanisms for inferring the internal states of other people, relying on multiple neural substrates, collectively referred to as "mentalizing" (Frith and Frith, 2006). The extent to which "simulation" versus "theory"-like mechanisms are used likely depends on the context, with simulation-like mechanisms perhaps coming into play

predominantly when we observe those people with whom we identify the most (Mitchell et al., 2006) or when we observe actions that are familiar (Brass et al., 2007) (but see Apperly [2008] for the view that the simulation/theory distinction is conceptual and unlikely to be resolved by data). That we would engage simulation-like mechanisms when we observe those people who are the most similar or emotionally close to ourselves makes intuitive sense and is borne out in studies of both pain (Singer et al., 2004) and reward observation (Mobbs et al., 2009).

The general issue of the extent to which central cognition draws upon motor and sensory representations in the brain, on the body itself, and on the external environment may be especially acute in the case of social cognition for a number of reasons (Adolphs, 2006). One reason is that the social environment (other people) is interactive: the simplest way to find out about somebody else's internal states is not necessarily through detailed observation, but through simply asking them how they feel or what they are thinking. A second reason may be that social information is so rich, or so dynamic in nature, that including the social environment in cognition makes possible the rapid updating of social knowledge that would otherwise be difficult to infer. To summarize this section: the "social brain" will likely need to include a widely distributed set of neural regions, diverse sets of neuronal subpopulations within them, and may encompass aspects of the body and the environment in cognition.

What Are the Psychological Processes?

The second big challenge highlighted by our historical consideration of phrenology above concerns the processes to be mapped themselves. The phrenologists came up with a list, mostly out of their own intuition. Cognitive psychologists and cognitive neuroscientists these days could produce lists of their own, and they would include terms such as "edge detection," "working memory," "error monitoring," "decision value," and so on. They would span many levels, from early perception to high-level self-reflection. There would be debate about the boundaries between them. So how can we map onto the brain processes whose computational nature and boundaries we do not yet understand? This is a deep and acute problem that has been realized for some time. In 1994, one of the first books illustrating the beauty and seduction of the kinds of images generated by neuroimaging noted tellingly, "The challenge for the future is to understand at a deeper level the actual mental operations assigned to the various areas.… Before this goal can be achieved, the experimental strategies used in PET studies must be refined so that more detailed components of the process can be isolated" (Posner and Raichle, 1994). This quote suggests an iterative strategy whereby neuroscience data can inform us of the psychological processes and whereby controlling and manipulating specific parameters can allow isolation of such processes, two key issues we comment on further below.

At a superordinate level, carving up social cognition has proceeded analogously to carving up cognition more generally. In particular, a host of dual-process models have been put forth. While these initially retained some resemblance to the original idea of controlled versus automatic processing as proposed from cognitive psychology (Schneider and Shiffrin, 1977), they have taken on a bewildering plethora of attributes, including a "system 1" purportedly emphasizing automatic, implicit, fast, nonconscious and emotional processing, and a "system 2" emphasizing the complements of these attributes (Evans, 2008). Within social cognition, the emphasis has been on a distinction between explicit and implicit processing, borrowing from social psychology, which has long emphasized the implicit nature of social attributions (Frith and Frith, 2008). The distinction has been linked to some extent also to self-referential and meta-cognitive abilities, partitioning the processing into "reflexive" versus "reflective" (Lieberman, 2007). While these dichotomies have been useful in nucleating research topics, there is a paucity of arguments or empirical data to suggest that they are the only or the best way of carving up the processing, and it seems doubtful that the often long

lists of correlated attributes should come as a package, except insofar as they are semantically related to begin with. However, there are few alternative schemes currently available, and the effort has instead focused on how to generate the richness and diversity of social cognition from combining the two types of processing. This ranges from thinking of them as mostly in opposition to one another (one can override the other) (Frith and Frith, 2008) to assigning them to distinct temporal components of social information processing to considering them as dynamically iterative (Cunningham and Zelazo, 2007).

One likely fallacy promoted by dual-process theories of social cognition is the idea that the two sets of processes constitute coherent systems of some kind. The set of attributes listed for one side of the dual-process dichotomy is typically simply the complement of the other; but definition by exclusion need not delineate any inherently related set of attributes (Keren and Schul, 2009). Take memory as a good example: declarative memory has been fairly cohesively defined and specific neural structures in the medial temporal lobe have been shown to be most important for it (although there is of course further fractionation within the domain of declarative memory, as well as continuing debates about how best to define its essential computational properties). By contrast, nondeclarative memory, defined by exclusion, is heterogeneous, including priming, Pavlovian conditioning, operant conditioning, motor learning, and so on. The situation with dual-process theories is even worse, since counterexamples to the proposed co-occurrence of attributes are easy to think of. Fast, nonconscious, and emotional attributes of “system 1” are a good example. There are many instances of each of these attributes within behaviors more typically associated with “system 2.”

Where does this leave dual-process theories of social cognition? One original conception (controlled versus automatic [Schneider and Shiffrin, 1977]) may still be the most useful and may isolate one particular aspect of social cognition: controlled, volitional, effortful, reflective processing (Lieberman, 2007). This aspect of social cognition is most perspicuous in adult humans, and some of its neural substrates in the prefrontal cortex have been the topic of intense investigation. It is possible that this metacognitive ability requires conscious awareness. It is unclear that it requires many of the other attributes, and it is unclear that it serves to nucleate a “system” of any sort, let alone specify a complementary one. To summarize this section: the process architecture of social cognition is still very much in need of a detailed theory, and alternatives to dual-process models should be pursued.

How Can We Map Processes onto the Brain?

Finally, even if and when we have sufficiently detailed data from functional neuroanatomy, and even if and when we have a mature social cognitive psychology of the relevant processes to be mapped, we need to ask what kind of relationship such a mapping should fall under. This question is acute, since despite the fact that neither brain circuits nor psychological processes are yet well delineated, the main enterprise of cognitive neuroscience, including social cognitive neuroscience, has in fact been to map the one onto the other. This is not as ill-founded an endeavor as it seems, since it may well be that it is only through iterative attempts at such mappings that we can identify what should be mapped in the first place; our understanding of mind and brain will come as a package.

Mapping social cognition onto the social brain often takes a subtractive strategy. For instance, in a seminal initial study of the brain regions that underly face processing, people were shown pictures of faces while fMRI data were acquired. The brain activation seen under this condition was then compared to a large number of other stimulus conditions that attempted to make comparisons and control for possible confounds, such as inverted faces, scrambled faces, hands, objects, and so on (Kanwisher et al., 1997). Recent fMRI studies in social neuroscience often compare social and nonsocial stimuli, as in the previous example, but they also compare

social and nonsocial tasks. Some manipulate both: for instance, participants are asked to form impressions of the stimuli they see or to remember their order of presentation (social versus nonsocial task) with respect to sentences describing people or objects (social versus nonsocial stimuli) (Mitchell et al., 2005). Such approaches have found good evidence that knowledge about people and objects is generated through different neural substrates (Mitchell et al., 2002), and there is now a large list of studies in a similar vein. Needless to say, these subtractive approaches have some limitations, since multiple differences distinguish the stimulus and task conditions and it is impossible to conduct a subtraction that is exhaustive. Another approach that may offer more insight is quasiparametric: rather than a dichotomous contrast, several levels of stimulus or task could be used. The challenge with this approach is that it is not straightforward how to parameterize a dimension of "socialness."

Ultimately, the mapping challenge can only be successful if it is accompanied by a corresponding change in the level of explanation of how stimuli link to behavior. This is not yet generally accomplished in most studies. For instance, many fMRI studies interpret activation in, for example, the insula or the ventral striatum as corresponding to a "disgust" or "reward" response, and explain behavior accordingly, examples of so-called "reverse inference" (Poldrack, 2006). Not only is this often unjustified, it is not really progress: the emotions thought to motivate behaviors have now simply been transposed into the brain, without any new insight into the underlying mechanisms. It will be a challenge for future studies to pay attention to this issue and to derive from the data a level of explanation at the process level that goes beyond the processes hypothesized at the outset.

It is possible to have a more paradigm-shifting view of how the mapping of mind to brain might proceed. Even once we have a useful, predictive process architecture for social cognition, many of those processes may map onto the brain only partly and disjunctively. Conversely, if we pick a brain "system," however defined, and ask what it does, the answer may end up being a hodge-podge of different processes. The hope is that such a situation would force us to reconsider the processes and come up with a computational theory that meshes better with the neuroscience. One would look toward the success in some parts of sensory neuroscience, where sophisticated ways of formulating and evaluating competing models lead to descriptions of which partition of a stimulus space is represented by a region or certain neurons in the brain (Wu et al., 2006). Some meta-analytic approaches are beginning to provide pictures in this spirit also for aspects of social neuroscience, such as answers to the question, "What activates the amygdala"? (Costafreda et al., 2008).

Even if we eventually come up with a computational account of how the social brain works that is truly aligned with the neuroscience data, it remains an open question what such an account would look like. It is possible that it would be so different from our intuitive categories for social behavior that it would literally be something that we could not presently understand. This is not necessarily because social cognition is inherently any more difficult to map onto the brain than any other aspect of perception or cognition. The problem is rather that we have an intuitive, "folk," understanding that grounds our theories of social behavior. The reason we can understand what social psychologists, or social neuroscientists, are talking about, is that the concepts used are to some extent continuous with our commonsense understanding of our minds and the minds of other people. If we have to jettison that continuity, we may end up with a theory of social behavior very different from the one we currently use in everyday life. On the other hand, the picture of the physical world that quantum mechanics provides shares these same considerations, and it is an intriguing possibility that a future social neuroscience would literally allow us to understand ourselves in an entirely different way.

To summarize this section: mapping social processing onto social brain structures may be an iterative way to make progress, bootstrapping our understanding of both even though each

requires revision. Varying the social nature of stimuli and processing demands has begun to produce such mappings, although it remains a big open question what its endpoint might look like.

Future Challenges

The quick tour of the terrain in social neuroscience we have taken so far points to some key open questions that future studies will need to consider and from which springs much of the current excitement in social neuroscience (Table 2). These revisit several of the points we raised earlier and serve to summarize and brainstorm for experiments to be done.

Isolating the Social

As we just discussed, social stimuli, and social tasks, inherently contain multiple properties. Which are unique to the social domain? If not unique, which sets of properties taken jointly can be used to isolate the social? This set of questions has a long history rooted in debates about the domain-specificity of social cognition. The most detailed empirical investigation has focused on face perception, with the well-known arguments on the one side that face perception features specialized psychological and neurobiological properties (Kanwisher and Yovel, 2006), and on the other side that it is a by-product of more general computational processing with demands that are not specific to the domain of faces (Tarr and Gauthier, 2000).

Attempts to isolate “social” processing typically proceed by holding stimuli constant and asking participants to engage in either a social (evaluative) or nonsocial task; or hold the task constant and vary the stimuli (social versus nonsocial). As we noted above, the challenge is in trying to isolate the social aspects from associated processing that is general: social stimuli may attract more attention, induce more emotional arousal, be more distinctive, and so on and so forth. One recent example is the question of whether or not social reward is processed in the same way as nonsocial reward. The question is part of the larger question that decision scientists are asking, whether there is a common currency for processing all different types of reward, such as money, food, or friendly people. Several studies have now compared social and monetary reward and generally produced conclusions that social reward overlaps at least partly with monetary reward in its neural implementation (Izuma et al., 2008; Zink et al., 2008), supplementing findings that social feedback (the reliability of information from other people) could be processed by associative mechanisms similar to reward feedback (Behrens et al., 2008), and revisiting the points we noted earlier in our discussion of neuroeconomics.

Yet confounds remain, because however the distinction between social and nonsocial is made by the experimenter, it consists of a large number of correlated attributes. This is not necessarily a problem for distinguishing social from nonsocial processing, but it pushes the question to a level deeper: we know that social and nonsocial cognition differ, at least to some extent. The question now is: why? Is it because social stimuli are less predictable? Is it because they are more salient? Is it because they are more emotionally arousing? These questions bring us back to the old debate about the domain specificity of face perception and confront us with the same dilemma. Either social cognition just poses a correlated set of computational demands, and is typically associated with a correlated set of effects, none of which are unique to social information; or else social cognition is domain specific, but it is difficult to isolate what the essential feature might be.

Uniquely Human Social Cognition

One of the motivating questions we considered above was the fascination of why humans appear so different from all other animals, behaviorally and in terms of relative brain size, a difference that is most frequently presumed to be traced to our different social cognition

(Dunbar, 1998; Humphrey, 1976). Comparative studies provide a rich set of data to address this issue (see Byrne and Bates [this issue of *Neuron*]), and social neuroscience has hypothesized some specific mechanisms and corresponding brain structures (Saxe, 2006a).

Developmental and comparative psychology has been stressing social learning mechanisms that may be unique to humans (Herrmann et al., 2007), although little is yet known about their neural basis. The findings emphasize the critical need for social context during early development. For instance, infants require the social presence of a person in order to learn early aspects of language (merely listening to the voice played from a tape recorder is not enough) (Kuhl et al., 2003). Social learning in humans is predicated on the expectation that others are interested in teaching and features generic-level knowledge that can be acquired through ostensive signals (Csibra and Gergely, 2009). There is vigorous debate about the types and extent of social learning mechanisms seen in other species, but humans may be unique in this respect. Interestingly, our closest living relatives, the great apes, may not be all that adept at learning from ostension, but dogs are (Miklósi et al., 2003).

Ultimately, one would want to link social cognitive abilities unique to humans to their correlates in the brain and in the genome. Of particular interest here would be comparative studies between humans and chimpanzees. There are now a number of behavioral studies (e.g., by Michael Tomasello and others at the Max Planck Institute in Leipzig), but very few neurobiological studies due to the difficulty of doing neuroscience in chimpanzees (see Parr et al., 2009, for an exception). With the recent sequencing of the chimpanzee genome, genetic differences can be pinpointed. It is of particular interest to note that there appear to be genes important for social cognition on the sex chromosomes (Skuse, 2006) and that both X (Khaitovich et al., 2005) and Y chromomosomes (Hughes et al., 2010) have diverged considerably between the two species (about 1/3 of the sequences of the male-specific region of the Y chromosome have no clear counterpart in the other species, for example).

The cognitive abilities of many other species can be impressive. For instance, chimpanzees can perform better than humans on some types of working memory tasks (Inoue and Matsuzawa, 2007), cephalopods (octopi, cuttlefish, squid) can camouflage themselves in the most clever ways (Hanlon, 2007), and corvids (jays and crows) take into account social observation, context, and time in caching food (Emery and Clayton, 2009). What differs in all these cases and human cognition is flexibility: we can typically apply many abilities to an unlimited number of different contexts, while other animals show more narrowly specialized abilities that cannot be transferred as easily to other domains. What brain mechanisms mediate this flexibility? Is it the way the components are interconnected? Is it due to an added “executive” metacognitive component? Both of these have been highlighted in a recent lesion study of the neuroanatomical substrates for general intelligence (Gläscher et al., 2010).

A perhaps related feature of human social cognition is the ability to exercise volitional control at multiple levels, so as to take into account a broader context. For instance, humans more so than other animals can forego a smaller immediate reward in order to obtain a larger future reward (a phenomenon economists have termed “temporal discounting”), an effect of the future timeframe on subjective valuation that correlates with neural signals in valuation regions of the brain such as the medial prefrontal cortex (Kable and Glimcher, 2007). Humans more so than other animals can regulate their emotional responses to one another in a strategic way; and humans will control their behavior to take into account the social context. A recent example of this is the finding that temporary disruption of activity in the right dorsolateral prefrontal cortex influences people's ability to build a good reputation. In that study, participants had to inhibit a prepotent strategy to behave selfishly if they wanted to obtain a good social reputation. This ability was impaired with repetitive transcranial magnetic stimulation (rTMS) of the right prefrontal cortex. The finding is in line with a larger literature suggesting that this region of

the brain is important for cognitive and emotional control and serves as a nice example of the importance that such control plays in regulating complex, planned, social behavior. It may be particularly this effortful, explicit component of social cognition that is elaborated in humans and that can regulate more automatic, implicit social cognition (Frith and Frith, 2008) (if we are willing to slide for the moment into the dual-process scheme for carving up cognitive processes). Another region highlighted in the higher-order control of behavior is the frontopolar cortex (Brodmann's Area 10), the very anterior region of the prefrontal cortex and the sector that shows the biggest relative increase between great apes and humans (Semendeferi et al., 2001). This region of the brain has been implicated by fMRI studies in keeping track of alternative courses of action and in motivating people to switch from one strategy to another when they feel that the current one is no longer the best (Boorman et al., 2009; Daw et al., 2006).

If the social cognitive abilities of modern humans are adaptive, it is somewhat puzzling that no other species appears to have evolved them. Clearly, there must be some costs associated with evolving those abilities. One obvious cost is the need for a large brain, metabolically expensive, time-intensive to train up, and difficult to give birth to biomechanically. There is another more intriguing conjecture: that some uniquely human aspects of cognition are potentially deleterious to the survival of the species. A recent letter to the editor in *Nature* hypothesized that full self-awareness brings knowledge of one's own mortality (and, for that matter, of one's kin and one's species), a possibly fatal piece of knowledge, full understanding of which would preclude any motivation to survive. The hypothesis continues that self-awareness could only have arisen in tandem with mechanisms such as faith and religion, which deny the existence of mortality and whose absence blocked the evolution of full self-awareness in all other species (Varki, 2009).

Effects of Context, Development, and Individual Differences

Historically, psychology sought to identify universals across different people. While that is still one theme, the tide has now turned to an emphasis on individual differences in the context of particular cultures and in the context of development. The stress of the role of development and environment has long been an emphasis in social psychology, but its translation to more cognitive and biological studies is a new theme. A good example here is the perception of emotions from facial expressions. Beginning with early observations by Charles Darwin (Darwin, 1965), psychologists in the 1970s and onward had argued (albeit not without heated debate) that this ability was universal across all human cultures (Ekman, 1994, 1973). Furthermore, it was assumed that there were similarly universal mechanisms at the level of brain and eye movements during the viewing of faces–although little had been done here in terms of cultural comparisons, there were data from nonhuman primates showing similarities to humans (Gothard et al., 2004; Keating and Keating, 1982). But more recent studies show specific cultural differences: Eastern Asian people, for instance, make more confusions between fear and disgust expressions that can be traced to a different pattern of fixations onto the faces, compared to Western Caucasian people (Blais et al., 2008; Jack et al., 2009).

Neuroscience studies of cultural differences in social cognition are very difficult to carry out with precision in isolating the source of the “cultural” differences. Technically, one would want to manipulate independently at least three different potential sources of variability, which are confounded in most studies: (1) differences in race (e.g., Asian versus Caucasian), (2) differences in cultural environment that the person grew up in (e.g., born and raised in Japan versus born and raised in America), and (3) differences in the environment in which the testing is done (e.g., being scanned by Japanese researchers in a lab in Tokyo versus being scanned by American researchers in a lab in Los Angeles). This 2 × 2 × 2 design would help pinpoint the sources of possible differences, although even this would leave open further questions since

all three factors are themselves complex. For instance, factor (1) consists of genetic effects that constitute race, and genetic effects correlated with race: the serotonin reuptake transporter polymorphism (5-HTTLPR, a polymorphism that has generated a large literature on its effects on emotion-related processing) differs systematically between Japanese and European populations, with the short allele considerably more prevalent in Japanese populations (~70% versus ~40% [Kim et al., 2007; Nakamura et al., 2000]). Factor (2) poses challenges nowadays since most people move from place to place during their lifetime and because cultures are no longer isolated from one another. For instance, it has been reported that Caucasian subjects show different activation of the amygdala by fear faces when these are shown on Asian or on Caucasian faces–but if Caucasian subjects had spent some time living in Japan, this pattern changed (Moriguchi et al., 2005). The role of language in shaping cognition has a long history with perhaps some of the clearest findings coming from studies showing that names for colors influence color categorization and discrimination (Berlin and Kay, 1991; Winawer et al., 2007). The dynamic effects of cultural environment are even more profound than these studies would suggest. In fact, responses to faces can change nearly instantaneously depending on what social group one identifies with (Van Bavel et al., 2008). With respect to factor (3) it seems likely that different testing environments will introduce yet another source of variability, a point long known from behavioral studies in mice (Crabbe et al., 1999). These considerations suggest that cultural neuroscience is wide open for detailed investigation, with a rich array of effects and interactions to be discovered–but care and effort will be required to tease them out.

In humans, a contextual challenge particularly acute for studies of social behavior is that participants in an experiment nearly always have knowledge that this is an experiment, with all the assumptions, expectations, and biases that this knowledge introduces. Other animals typically require no elaborate deceptions and treat all experiments like the real thing. A good example of the powerful effects of people's beliefs on social behavior is provided in a recent study of the effects of testosterone on social behavior in bargaining situations. Women who were given testosterone showed fairer bargaining behavior, somewhat counterintuitively. However, women given placebo who believed they had been given testosterone also showed a change in bargaining behavior–but in the opposite direction: they were less fair in their behavior, in line with people's stereotypes about the effects of testosterone (Eisenegger et al., 2010).

Limits and Applications of Social Neuroscience

What are the limits of what social neuroscience can investigate? Are there limits to what it should? And how can we use it to make the world a better place? This final set of questions of course does not admit of much in terms of an answer yet, but this should not stop us from speculating.

With respect to the first question, a healthy optimism would suggest no limits in principle: social neuroscience is the way to understand all social behavior. However, this optimism should be tempered with interdisciplinary tolerance, since fields from other social sciences, from engineering, and from computer science will certainly all have something to contribute. Especially some of the nonclinical applications of social neuroscience will need to liaise closely with these other disciplines: recommendations for public policy or designs for better social computer interfaces and intelligent robots are all issues on the not-too-distant horizon. None of them can be addressed by social neuroscience alone.

Some of these examples may seem more like science fiction, but they are here already. For instance, a recent study considered cooperative behavior in the context of public goods (Krajbich et al., 2009). A mathematically and empirically solid result from the field of mechanism design had long shown that certain public goods problems were intractable: no incentives were possible that would result in stably optimal compliance to contribute to the

good. The study used fMRI decoding methods to "read-out" the value that a particular option had for the participant and used this value in setting the public goods policy. Participants were informed of this effect, with the result that perfect compliance was achieved, a result that was previously considered impossible.

Examples like this, however, raise the second question: do we want this kind of contribution from social neuroscience? Objections trace back to our deep-seated mistrust of biologically deterministic accounts that seem to challenge our freedom. The reaction to some of the recent attempts to determine from neuroimaging data whether people are lying or telling the truth, or what their political beliefs are, illustrate the point (e.g., Aron et al., 2007). Of course, scientists typically do not cite offense to their sense of liberty as the reason and instead produce (valid) arguments about the flawed methodology, typically pointing out that one cannot determine anything with statistical reliability from an individual's brain and that at best group effects can be shown. And group effects have indeed been shown: there are differences in judgments of competence (Todorov et al., 2005) and in brain responses (Spezio et al., 2008) when people view the faces of (unfamiliar) politicians who have lost real elections as compared to faces of (unfamiliar) politicians who have won real elections. There are psychophysiological differences between liberal and conservative groups (Oxley et al., 2008). There are legal implications about social psychological (Gray et al., 2003) and neuroscience data (Greene et al., 2004; Koenigs et al., 2007) regarding people's sense of right and wrong. It is just a matter of time before the signal-to-noise ratio of the methods allows us to make statements at the level of the individual, and so it is indeed time to begin thinking about the responsible use and interpretation of findings from social neuroscience.

These last considerations also stress the impact that social neuroscience is likely to have–on domains ranging from the clinical to engineering to legal. This is part of what makes the field so exciting and what is drawing in young scientists from such diverse backgrounds. While I have highlighted many of the challenges faced by the field, these are being tackled with vigor. Perhaps one closing caveat would be in order: social neuroscience is so successful that it is at risk of losing its roots. It will be important to continue to collaborate closely with neurobiologists working in all species of animals, not just humans, just as it will be important to collaborate with social psychologists. And debate and discussion requires input from all relevant fields, including philosophy, psychology, biology, economics, and computer science. Social neuroscience straddles many disciplines, but it needs all of them in order to address the conceptual issues I have discussed here.

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Figure 1. Two Eusocial Species

Eusociality refers to the rigid and highly organized colonial behavior seen in some insect species, such as ants, termites, and bees. It involves overlapping generations, cooperative care of the young, and specialized castes, including allocation of reproduction. On the face of it, its evolution seems impossible, since an individual's advantage in passing on its genes should always trump its eusocial role as a nonreproductive caste. However, some insects with haplodiploidy (where the number of chromosome copies determines sex) feature the interesting phenomenon that an individual may be genetically more closely related to a sibling than to their offspring, raising the possibility that kin selection can drive the evolution of eusociality. However, even this does not seem enough, and group selection (i.e., at the level of the entire colony) appears to be necessary and may in fact be the key driving force for the emergence of eusociality (Wilson and Hölldobler, 2005). This requires several convergent criteria that favor cooperation and can be considered a highly advanced transition into a tightly colonial existence often called a “superorganism.”

Evidently, it is very difficult for eusociality to arise, but once established it is extremely successful and stable. For instance, out of the over 2600 families of artho-pods, only 15 contain eusocial species. Ants and termites comprise only about 2% of insect species, yet they constitute over half of the globe's total insect biomass. In vertebrates, eusociality only exists in two species of mammals, both mole rats found in Africa. Intriguingly, some of the conditions for the evolution of eusociality and for the highly cooperative behaviors of eusocial species have been suggested to be present in humans as well, raising the possibility that group selection and a transition to a different form of collective existence may be at play in our species as well.

(Left) The naked mole rat, *Heterocephalus glaber*, one of only two eusocial mammals. These rodents have social structures similar to those seen in bees and ants: a single breeding queen and division of sexual reproduction and labor among all the individuals within a subterranean hive. Naked mole rats cannot live for long left on their own and require the specialized cooperative behaviors of other members of their colony to thermoregulate, obtain food, and defend against potential predators. They are also fascinating because they have the longest lifespan of any rodent and a surprisingly large brain specialized for somatosensory and olfactory processing (image by Rochelle Buffenstein) (Jarvis and Sherman, 2002).

(Right) Excavation of a leafcutter ant nest by Bert Hölldobbler and colleagues, showing the intricate way in which this “superorganism” has structured its environment. Photo by Wolfgang Thaler from Hölldobler and Wilson (2008).

Table 1

Stages of Social Information Processing

Social Perception	**Social Cognition**	**Social Regulation**
pheromones	theory of mind	cognitive control
face perception	simulation	emotion regulation
speech perception	empathy	monitoring/error correction
social touch	social judgment	self-reflection
biological motion	moral judgment	deception
Potential Attributes		
fast	inferential	individual differences
automatic	automatic	controlled and effortful
implicit	uniquely human	uniquely human
domain specific	context sensitive	very context sensitive
labeled lines	biased	impaired in psychiatric illness

Three broad stages of processing outlined in the main text are provided with some examples, and with some of the attributes and roles they are often proposed to have.

Table 2

Open Questions

A Partial Sampling of Big Conceptual Questions for Social Neuroscience	
1	What are the social processes? In particular, are they computationally distinct from those that process nonsocial information? Are there a set of processes that delineate the "social mind," analogously to how there might be a set of structures for the "social brain"? Social psychology has generated a number of candidates, but it is unclear how these will be incorporated into a future social neuroscience.
2	What is the social brain? Is there even a "social brain," a set of structures specifying a neural system for processing social information? Key structures proposed include parts of the temporal cortex (fusiform gyrus, superior temporal gyrus, and sulcus) involved in aspects of social perception, medial prefrontal cortex and temporoparietal junction involved in theory of mind, and posterior cingulate and medial parietal cortex involved in perspective taking and self-reflection.
3	Is there specialization for social processing below the systems level of question 2? Von Economo neurons, a particular morphological cell type found in frontoinsular cortex in apes and humans (as well as some whales and elephants) have been proposed to subserve the long-distance signaling that underlies integration of information from spatially distal parts of the brain necessary for social cognition (Allman et al., 2002). Oxytocin has been proposed as a key neuromodulator for affiliative social behaviors in mammals; receptor subtypes for several biogenic amines such as serotonin have also been noted to subserve important roles in social processing. These findings in particular have great promise for pharmacological intervention of psychiatric illnesses affecting social functioning.
4	What social abilities might be impossible for humans? The flip-side of the question of which social abilities are unique to humans is the question of whether there is anything we could not learn to do. Could we all learn to live together in peace and cooperation, or would our very cognitive flexibility always preclude anything approaching eusocial collective behavior? This question could also be seen as related to a question about the bounds of cognitive and emotional regulation: if we realized the metacognitive need for a particular social behavior, do we have the control to implement it volitionally?
5	How could we best change our social behavior? Questions 3 and 4 point toward this question but neglect the role of context and our power to modify our environment. Rather than trying to change the way our brains work, we could think about changing our environmental and social context so as to change our social behavior. Clever changes in public policies (such as incorporating neuroscience data together with tools from mechanism design to achieve optimal public goods compliance [Krajbich et al., 2009]), ubiquitous education, and strategic design of economic and political structures could all contribute toward such a goal in principle.